5.—The order of cusp development on the molar teeth of Setonix brachyurus (Macropodidae: Marsupialia)

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Abstract

The order of cusp development and cusp calcification in the upper deciduous premolar of *Setonix*, and most probably the upper first molar, resemble that occurring in placentals, the paracone representing the primary cusp. The primary cusp in the lower deciduous premolar of *Setonix*, and perhaps also in the lower second molar, was the metaconid, differing from that of placentals, while in the lower first molar the primary cusp was the protoconid. During the early stages of tooth development the upper deciduous premolar and first molar were more advanced in their development than the corresponding lower teeth.

Introduction

A detailed study of the order of cusp development on the cheek teeth of the Macropodidae has never been carried out and little information is to be found concerning cusp development in other marsupials. In some marsupials, namely *Myrmecobius, Peragale (Macrotis)* and *Phascogale*, Woodward (1896) found the upper primary cusp to be the paracone and the lower primary cusp to be the protoconid. According to Röse (1892), the metacone of the upper deciduous premolar of *Didelphis* calcified before the paracone, while the first cusp to be added to the protoconid of the lower teeth was the metaconid. In the first upper molariform tooth of a specimen of *Perameles*, Bolk (1917) found the paracone, protocone and metacone present, the former two cusps being calcified.

The lower deciduous premolar of certain members of the Phalangeroidea, e.g. *Hypsiprymnodon*, possesses real evidence of only one anterior cusp which is generally displaced lingually, giving the tooth a wedge-shaped appearance when viewed from above; the homology of this anterior cusp is the subject of dispute (Ride 1961). The determination of the homology of the cusps of the lower deciduous premolar in *Setonix brachyurus*, which is similarly wedge-shaped, possessing a prominent antero-lingual cusp and a greatly reduced antero-buccal cusp, may help to indicate the homology of the single anterior cusp in other members of the Phalangeroidea.

The dentition of Setonix brachyurus

The animal used for the present study was *Setonix brachyurus*, the quokka of Western Australia.

Simpson (1945) placed *Setonix* in the Superfamily Phalangeroidea, Family Macropodidae, and the Subfamily Macropodinae. Other classifications have been suggested by Thomas (1888), Bensley (1903), Gregory (1910), Jones (1924), Raven and Gregory (1946), Tate (1948) and Ride (1957, 1964). *Setonix* may be regarded as representing a monotypic genus related to the wallabies. Recent work by Sharman (1954) on the chromosome structure and the urino-genital characteristics of *Setonix* have led him (1961) and Ride (1957) to consider the possibility that *Setonix* may be more closely related to the rat-kangaroos than to the more advanced Macropodinae.

The dental formula of *Setonix*, excluding the deciduous premolar, is:— $I\ ^3/_1\ C\ ^0/_0\ Pm\ ^2/_2\ M\ ^4/_4$, and is characteristic of members of the Macropodinae. Owing to its large size, the replacing premolar in *Setonix* replaces the anterior premolar in addition to the deciduous premolar, so that only one sectorial premolar is functional at a time.

Setonix resembles the wallabies and differs from the true kangaroos in possessing:

(a) large sectorial premolars which remain functional throughout life,

(b) a fourth molar tooth which is slightly smaller than the third,

(c) a comparatively small upper third incisor.

Setonix also possesses large posterior palatal vacuities, and a large masseteric canal the size of which appears to be related to the size of the sectorial premolars (Ride 1959).

The terminology used for the transverse ridges of the teeth is that given by Scott and Symons (1958).

Morphology of the molar teeth

Upper jaw (Fig. 1, left)

The anterior and posterior pairs of cusps have united to form two transverse ridges or lophs. The anterior loph or paraloph is formed by the union of the anterior pair of cusps, the buccal paracone and lingual protocone, while the posterior loph or metaloph is formed by the union of the posterior pair of cusps, the buccal metacone and lingual hypocone. The two lophs are united by a narrow longitudinal ridge. The lophs are curved with the convexity facing anteriorly. A small anterior cingulum is present.

The molar teeth show a general increase in size from before backwards, but the third molar is slightly larger than the fourth. The fourth molar lies more lingual than the third, so that the toothrow curves towards the sagittal plane at its posterior end.

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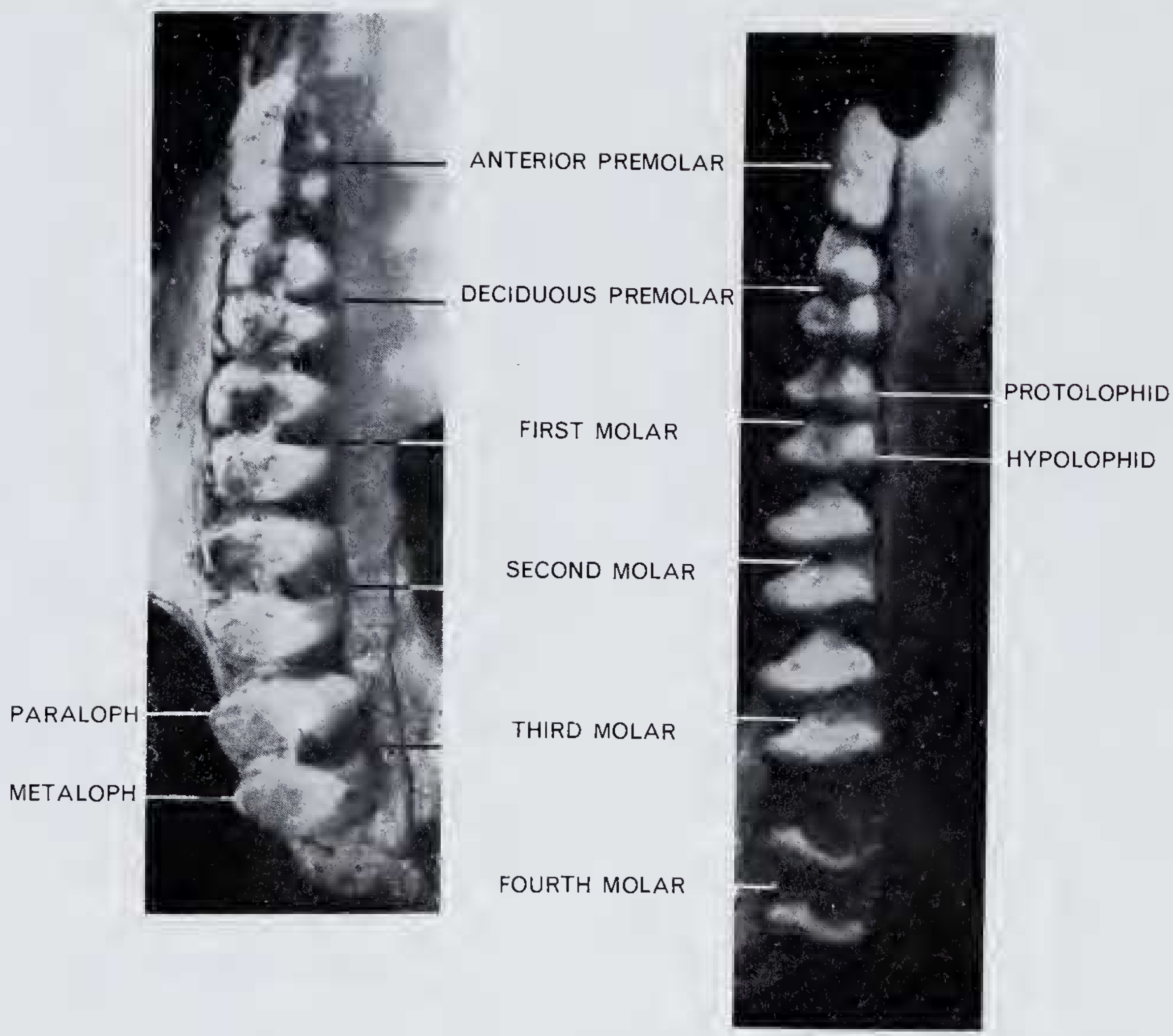

Figure 1.—(Left hand side) Upper right anterior cheek teeth, x3.8. (Right hand side) Lower left cheek teeth, x3.5.

In the case of the deciduous premolar the paraloph is not as well developed as in the other molar teeth, a shallow groove being present on the anterior as well as the posterior surface, and the anterior margin of the paracone rises to form a conspicuous ridge which is functionally continuous with the median longitudinal ridge of the anterior premolar.

Lower jaw

The anterior and posterior pairs of cusps combine to form two transverse ridges or lophids. The anterior lophid or protolophid is formed by the anterior cusps, the buccal protoconid and lingual metaconid, while the posterior lophid or hypolophid is formed by the posterior cusps, the buccal hypoconid and lingual entoconid. The two lophids are united by a narrow longitudinal ridge. The lophids are curved with the convexity facing posteriorly, this being opposite to the condition found in the upper molars. The anterior margin of the protoconid rises to form a narrow ridge. The relative size and position of the lower molar teeth are similar to the upper molars.

In the case of the deciduous premolar the protolophid is greatly diminished in its buccolingual dimension due to the reduction in size of the protoconid, giving the tooth a wedge-shaped outline when viewed from above.

Materials and methods

Table 1 lists the pouch young specimens of *Setonix* used in the study together with their accompanying data.

TABLE 1

List of pouch young specimens of Setonix brachyurus *used in the present study.*

Specimen and Stage No.	Estimated Age from Birth (days)	Body-weight (grams)	Snout-occiput Length (mm)
1	< 7	0.69	8.5
2	< 11	1.153	10.1
3	25	3.0	12.1
4	30	4.5	16.1
5	40	8.0	19.1
6	46	10.0	21.8
7	52	16.0	25.5

As the specimens were obtained during reproductive studies by other workers, their ages were known. The specimens had been fixed in Baker's formol-calcium and preserved in 70% alcohol. X-rays revealed that no decalcification was necessary prior to sectioning. Sectioning was carried out in a transverse plane using a rotary microtome set to cut at 10μ, the heads being embedded in wax. Masson's trichrome was the stain used. Predentine could be distinguished from mature dentine according to the colour of the staining reaction.

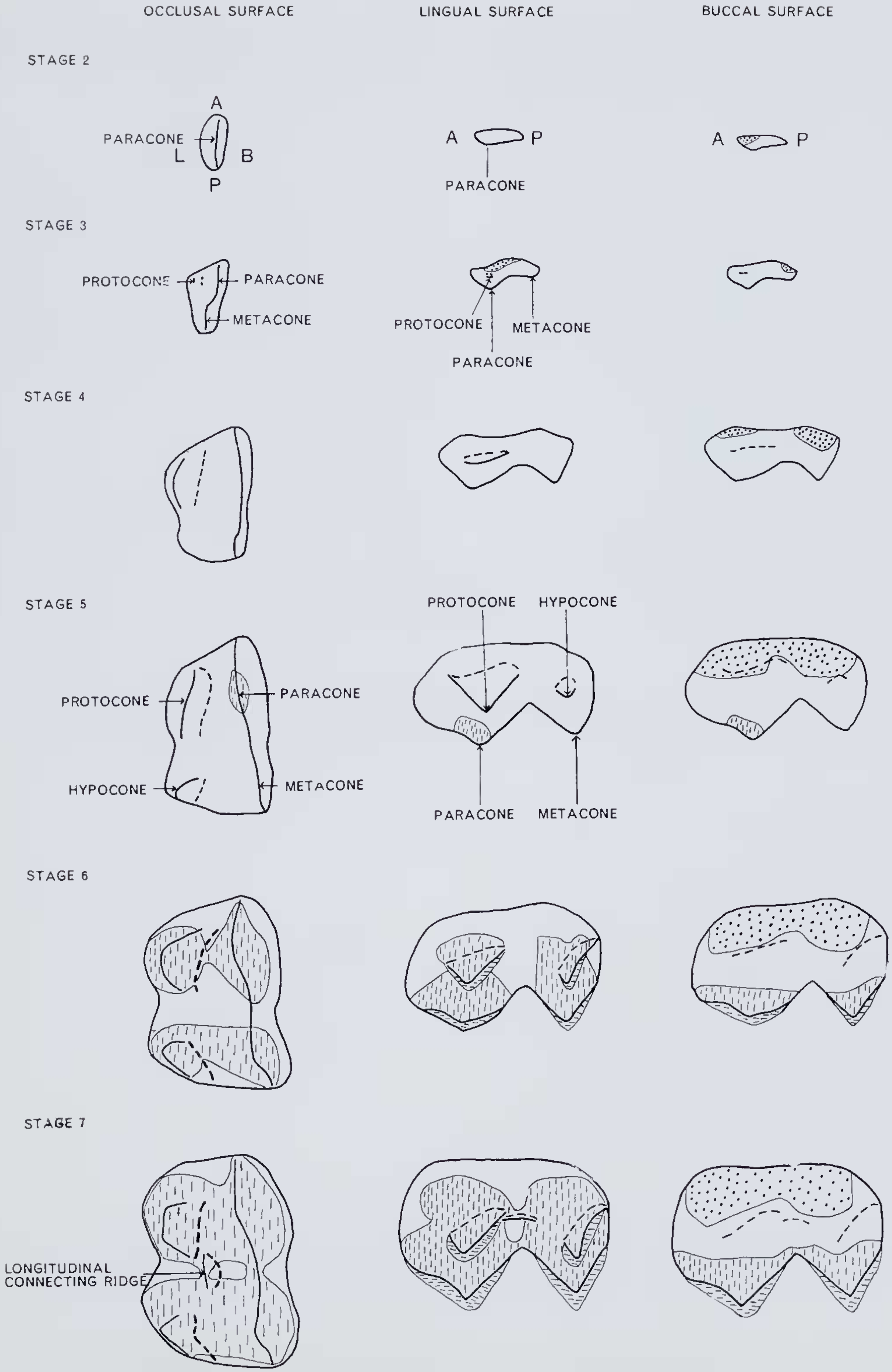

Figure 2.—Development of the upper deciduous premolar. Stages 2-5 x12.5, stages 6 and 7 x10. In all figures: A = anterior, B = buccal, L = lingual, P = posterior, vertical line stipple = dentine, horizontal line stipple = enamel, heavy dot stipple = pulp aperture.

Reconstructions of the teeth were carried out by the graphical method in occlusal and side views, and where necessary supplemented by the construction of three-dimensional wax models. The techniques and precautions taken for these reconstructions were identical to those adopted by Aldridge (1962), using the base of the wax block as a guide line.

Results

Cusp development in the molar teeth

The deciduous premolar was first seen developing from the free edge of the dental lamina at the posterior end of the developing jaw at stage 1. The first molar developed behind the deciduous premolar and was continuous anteriorly with the residual dental lamina lying to the lingual side of the deciduous premolar. The second molar developed behind the first molar and was continuous anteriorly with the residual dental lamina lying to the lingual side of the first molar.

Upper Jaw

Deciduous Premolar (Fig. 2). This tooth reached the cap stage of development at stage 2. The first cusp to develop was the paracone which was clearly visible at stage 3. Although traces of the protocone and metacone were observed at stage 3, these cusps first became conspicuous at stage 4, having developed at approximately the same time. The last cusp to develop was the hypocone which appeared at stage 5.

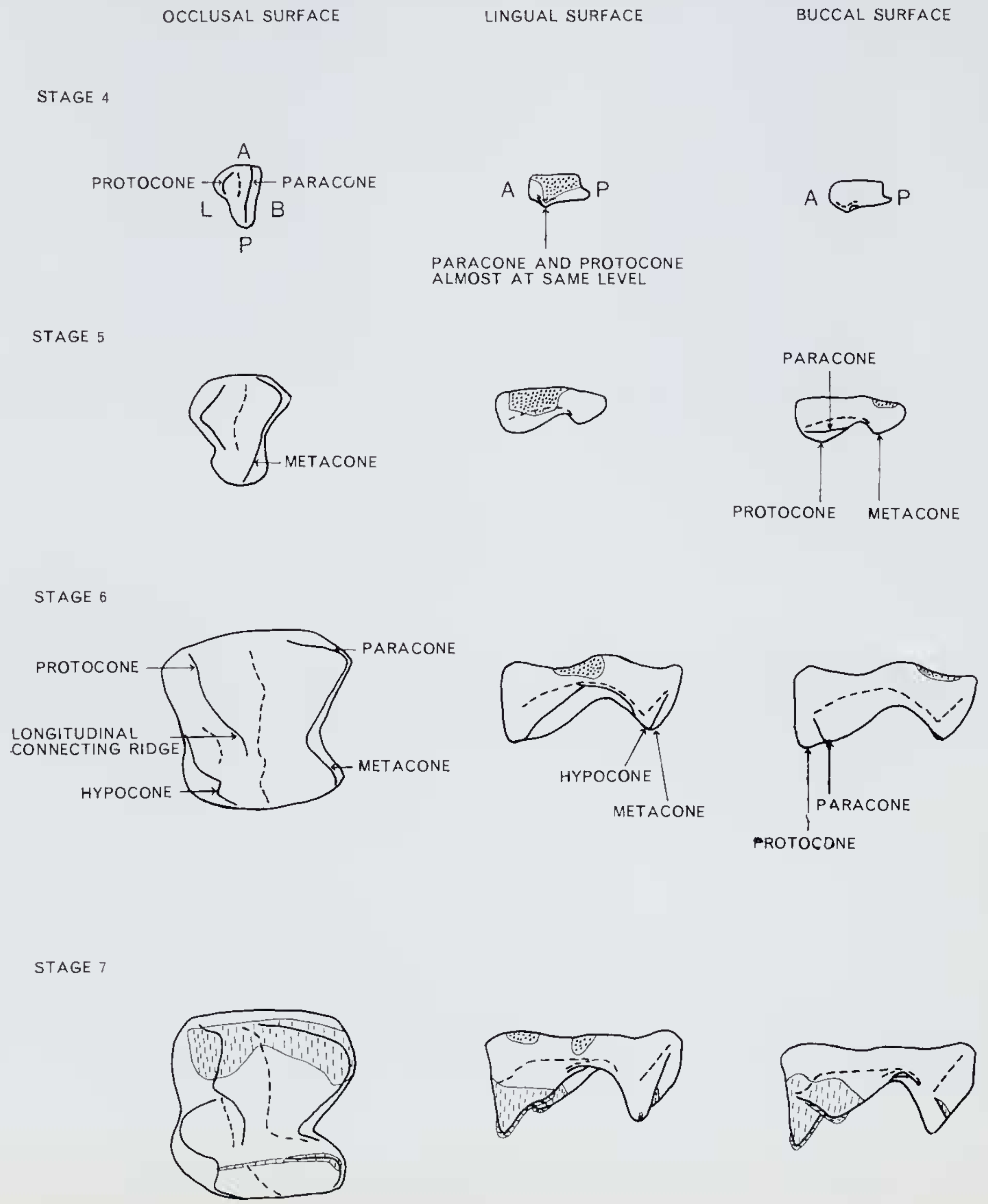

Figure 3.—Development of the upper first molar. Stages 4-6 x12.5, stage 7 x10. For key see caption of Figure 2.

The first cusp to calcify was the paracone, which at stage 5 possessed a layer of dentine at its apex. At stage 5 a small amount of predentine had been deposited at the apex of both the protocone and metacone, indicating that these two cusps commenced the process of calcification after the paracone and at approximately the same time as each other. The last cusp to calcify was the hypocone at stage 6.

First Molar (Fig. 3). The cap stage of development for this tooth was reached at stage 3. At stage 4 two cusps were present on the crown, corresponding to the paracone and protocone; the paracone was slightly more prominent and, developing from the main ridge, almost certainly represented the primary cusp. The third cusp to develop was the metacone which appeared at stage 5. The last cusp to develop, the hypocone, was seen initially at stage 6.

At stage 6 predentine had been formed in the apical region of both the protocone and paracone, the presence of a very small amount of dentine on the paracone indicating that the paracone probably commenced calcification just before the protocone. At stage 7 a small amount of dentine had been formed at the apex of both the metacone and hypocone and along the crest of the metaloph, most of this dentine being associated with the apex of the metacone, indicating that the metacone was the third cusp, and the hypocone the last cusp to calcify.

Second molar. This tooth reached the cap stage of development at stage 6. At stage 7 the enamel organ of the tooth was still small, although traces of three low cusps apparently corresponding to the paracone, protocone and metacone, were present on the crown.

Lower jaw

Deciduous Premolar (Figs. 4 & 5). The cap stage of development of this tooth was reached at stage 2. At stage 4 three cusps, namely the metaconid, protoconid and hypoconid, were present on the crown, and of these cusps the

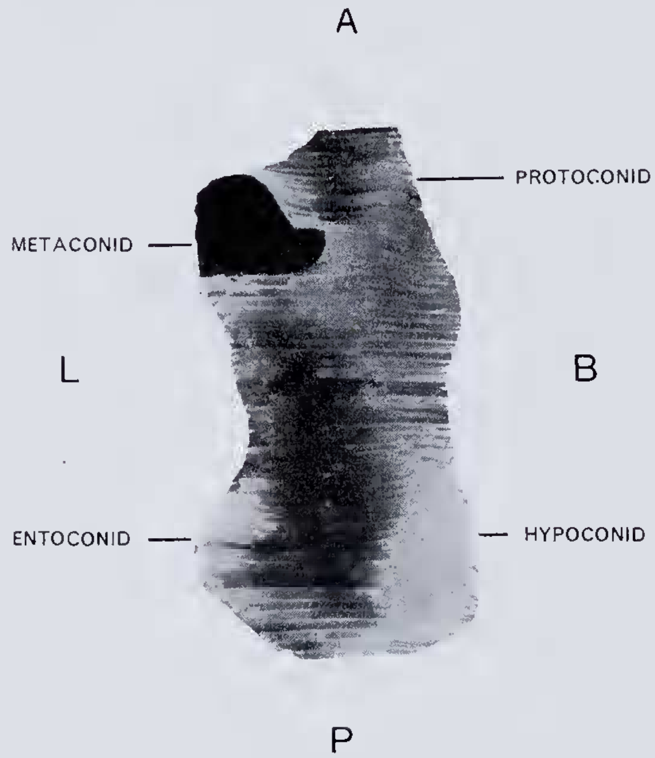

Figure 4.—Wax reconstruction of the lower deciduous premolar at stage 5, x34. Black area indicates dentine formation.

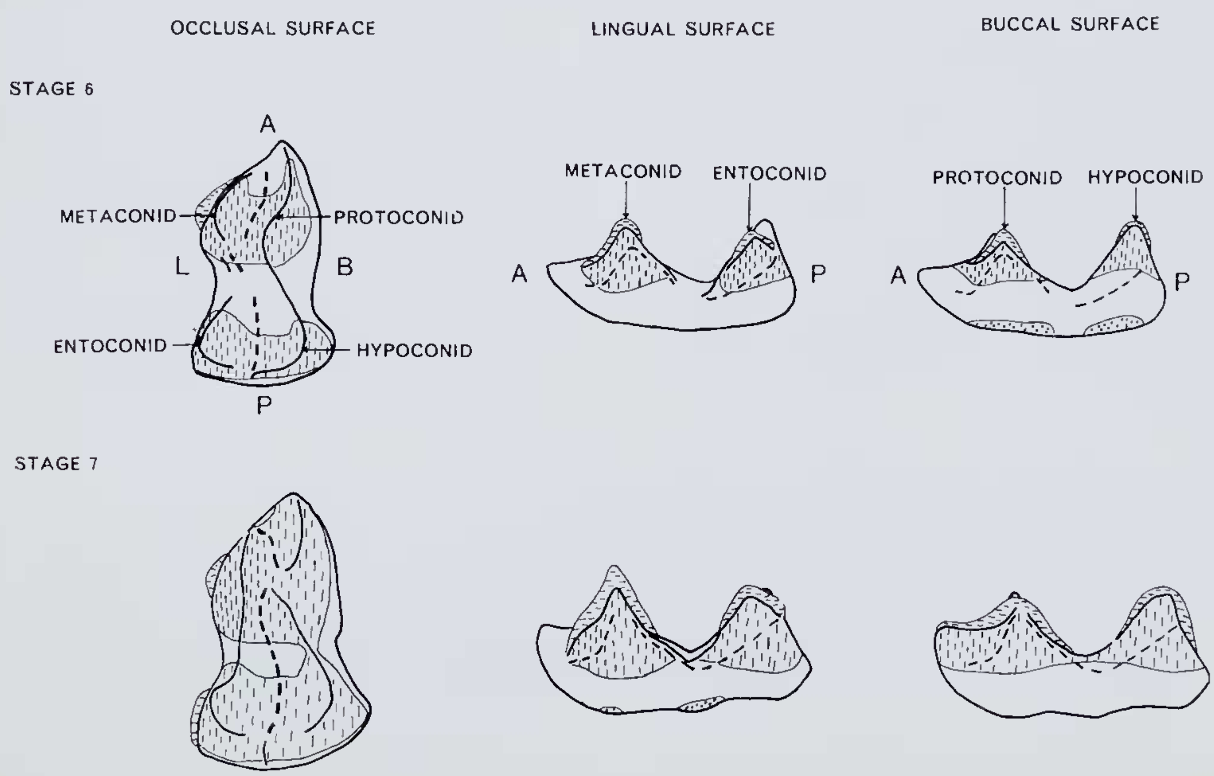

Figure 5.—Development of the lower deciduous premolar at stages 6 and 7, x10. In lateral views only the calcified tissue associated with the nearest cusp is illustrated. For key see Figure 2 caption.

metaconid was by far the most prominent. The last cusp to develop was the entoconid which appeared at stage 5.

The first cusp to calcify was the metaconid which possessed a conspicuous layer of dentine at stage 5. At stage 5 the protoconid contained a layer of predentine which was continuous along the crest of the protolophid with the predentine layer associated with the metaconid. This indicated that the protoconid was the second cusp to commence calcification. The hypoconid and entoconid were the last cusps to calcify, both being calcified at stage 6.

First Molar (Fig. 6). This tooth reached the cap stage of development at stage 3. At stage 5 three cusps were present on the crown, namely the protoconid, metaconid and hypoconid. The protoconid, lying anterior to the metaconid, was slightly more prominent than the other cusps. The last cusp to develop, the entoconid, appeared at stage 6.

At stage 6 predentine had been deposited in the apical region of both the protoconid and metaconid, the greater quantity of predentine being associated with the protoconid, indicating that the protoconid commenced the process of calcification slightly before the metaconid. At stage 7 the apical region of the hypoconid contained a thin layer of dentine which extended across the crest of the hypolophid to become continuous with dentine at the apex of the entoconid. The greater amount of dentine associated with the hypoconid indicated that the hypoconid was the third cusp, and the entoconid the last cusp to calcify.

Second molar. This tooth reached the cap stage of development at stage 6. At stage 7 only two cusps were present on the crown, apparently corresponding to the metaconid and protoconid, the metaconid being the more prominent cusp.

The order of cusp development and cusp calcification on the molariform teeth in *Setonix* is summarised in Tables 2 and 3.

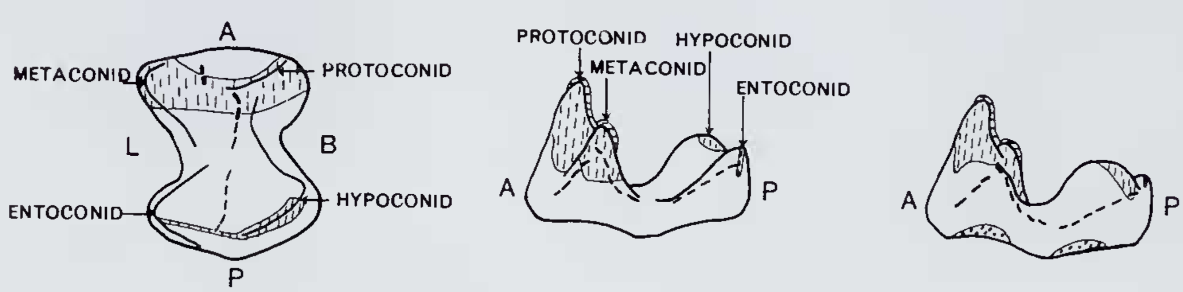

Figure 6.—Lower first molar at stage 7, x10.

Discussion

Development of upper molars

The main difference between the development of the deciduous premolar and the first molar is the accelerated development of the protocone which occurs in the first molar and which is probably associated with the more completely formed paraloph present in the first molar.

The order of cusp calcification appears to be closely related to the order of cusp development which resembles that occurring in placentals, the paracone representing the primary cusp and the hypocone being the last cusp to develop (Butler 1956).

Development of lower molars

A most important difference is observed between the development of the deciduous premolar and the first molar, for while the protoconid is slightly more prominent than the metaconid and is the first cusp to calcify on the first molar, the situation is reversed in the deciduous premolar where the metaconid is much more prominent than the protoconid and is the first cusp to calcify. This difference in development appears to be related to the small size of the protoconid on the deciduous premolar.

TABLE 2

Order of cusp development and cusp calcification in the upper jaw of Setonix brachyurus.

	DECIDUOUS PREMOLAR	FIRST MOLAR	SECOND MOLAR
ORDER OF CUSP DEVELOPMENT	1. Paracone (stage 3) 2. Protocone, Metacone (stage 4) 4. Hypocone (stage 5)	1. Paracone, Protocone (stage 4) 3. Metacone (stage 5) 4. Hypocone (stage 6)	1. Paracone, Protocone, Metacone? (stage 7)
ORDER OF CUSP CALCIFICATION	1. Paracone (stage 5) 2. Protocone, Metacone (stage 5) 4. Hypocone (stage 6)	1. Paracone, Protocone (stage 6) 3. Metacone (stage 7) 4. Hypocone (stage 7)	

TABLE 3

Order of cusp development and cusp calcification in the lower jaw of Setonix brachyurus.

	DECIDUOUS PREMOLAR	FIRST MOLAR	SECOND MOLAR
ORDER OF CUSP DEVELOPMENT	1. Metaconid (stage 4) 2. Frotoconid, Hypoconid (stage 4) 4. Entoconid (stage 5)	1. Protoconid, Metaconid Hypoconid (stage 5) 4. Entoconid (stage 6)	1. Protoconid, Metaconid? (stage 7)
ORDER OF CUSP CALCIFICATION	1. Metaconid (stage 5) 2. Protoconid (stage 5) 3. Hypoconid, Entoconid (stage 6)	1. Protoconid (stage 6) 2. Metaconid (stage 6) 3. Hypoconid (stage 7) 4. Entoconid (stage 7)	

If the early height of a cusp and the time of its calcification relative to that of the other cusps are expressions of the order in which cusps develop in the first place, then the primary cusp in the deciduous premolar is the metaconid while that in the first molar is the protoconid. Thus, in *Setonix*, not only is there a difference in the order in which cusps calcify on the crowns of these two teeth, but this might be held to indicate that the primary cusps in them are different, the primary cusp in the deciduous premolar being the metaconid and in the first molar the protoconid. Such a conclusion would also mean that the primary cusp in the deciduous lower premolar of *Setonix* differs from that of the typical lower molar of placentals where the primary cusp is the protoconid (Butler 1956).

As an alternative explanation, however, the late calcification of the protoconid of the deciduous tooth, or the precocious calcification of the metaconid, might be only an expression of the much reduced size of the protoconid in the deciduous premolar of *Setonix*. Thus, in the deciduous premolar, the protoconid could develop first but the metaconid appearing later would soon outstrip the protoconid in development, rapidly becoming the most prominent cusp and reaching the stage of calcification earlier. If this is true, then the early height of a cusp and its time of calcification, which normally allow the identification of the primary cusp, need not necessarily indicate the correct order of cusp development (see Butler 1956). The order of cusp development can only be determined if a series of specimens is obtained clearly showing the cusps developing one after another; the difficulty in obtaining such a series is considerable, especially in cases where two or more cusps appear almost simultaneously.

In the oldest specimen examined in the present study, i.e., stage 7, the crown pattern of the lower second molar was incomplete and only two cusps were present on the crown. The homology of these two cusps cannot be determined with certainty unless further study is carried out on older specimens. However, it is suggested that these two cusps represent the protoconid and metaconid, the metaconid being the most prominent. If the early height of a cusp is a factor which may indicate the order of cusp development, then the metaconid may represent the primary cusp. This interpretation would involve accepting a difference in the order of cusp development between the first and second molars, the primary cusp in the first molar being the protoconid and in the second molar, the metaconid. The alernative interpretation is that the protoconid is the first cusp to develop, but the metaconid, which appears after the protoconid, develops at a greater rate than the primary cusp and becomes more prominent. This latter interpretation would account for the apparent difference in development between the first and second molars but, as in the case of the deciduous premolar, would indicate that the early height of a cusp is a factor which does not denote the order of cusp development. Although the order of cusp development in the second molar may resemble that of the deciduous premolar, this cannot be confirmed until older specimens are examined.

The features of the lophs and lophids of the upper and lower molar teeth of *Setonix* were conspicuous as soon as the constituent cusps were present on the crown.

The accelerated development and calcification of the metaconid in the lower deciduous premolar may be regarded as positive factors favouring Ride's (1961) cuspal nomenclature of the lower cheek teeth of *Hypsiprymnodon* in which the main anterior cusp in the lower deciduous premolar is regarded as being the metaconid. The initial results of a study of the development of the cheek teeth of *Trichosurus vulpecula* carried out by the author support Ride's views.

A comparison between the development of the corresponding upper and lower molar teeth

Deciduous premolars. During the early stages the upper deciduous premolar is seen to be at a more advanced stage of development than the lower deciduous premolar. At stage 3 the paracone is conspicuous on the crown of the enamel organ of the upper deciduous premolar and the protocone and metacone are about to appear, while upon the smaller enamel organ of the lower deciduous premolar no cusps are visible. At stage 4 the enamel organs of both teeth possess three cusps, the paracone, metacone and protocone being present in the upper tooth, and the metaconid, protoconid and hypoconid being present in the lower tooth. At stage 5 four cusps are present in both teeth. Calcification has commenced in the upper tooth with the formation of dentine at the apex of the paracone and predentine at the apex of the protocone. In the lower tooth calcification has also commenced, but dentine is formed on the metaconid, while only predentine is present on the protoconid. Predentine has also been formed on the metacone of the upper tooth at stage 5, but has not been formed on either of the posterior cusps of the lower tooth. At stage 6 both upper and lower teeth are at approximately the same stage of calcification, enamel and dentine being present on all four cusps.

First molars. At stage 4 the enamel organ of the upper tooth exhibits two low cusps on the crown, the paracone and protocone, while the ridge of the enamel organ of the lower tooth shows no cuspal elevations. In later stages the two teeth are at approximately the same stage of development.

Second molars. As in the oldest specimen examined, i.e., stage 7, these teeth were still only present as small enamel organs with incomplete crown patterns, no comparison will be made between them.

During the early stages the upper deciduous premolar and first molar are more advanced in their development than the corresponding lower teeth. In this respect *Setonix* differs from the Microchiroptera where Aldridge (1962) found that it was the lower molar teeth which were in a more advanced stage of development than the corresponding upper molar teeth.

Summary

(1) The order of cusp development on the molar teeth was studied in a transversely sectioned series of pouch young of *Setonix brachyurus*.

(2) The order of cusp development and cusp calcification in the upper deciduous premolar, and most probably the upper first molar, resembled that occurring in placentals, the paracone representing the primary cusp.

(3) The primary cusp in the lower deciduous premolar, and perhaps also in the lower second molar, was the metaconid, while in the lower first molar the primary cusp was the protoconid.

(4) During the early stages of tooth development the upper deciduous premolar and first molar were more advanced in their development than the corresponding lower teeth.

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